2000. The Journal of Arachnology 28:180–184

EVALUATION OF FORMULAE TO ESTIMATE THE CAPTURE AREA AND MESH HEIGHT OF ORB WEBS (ARANEOIDEA, ARANEAE)

Marie Elisabeth Herberstein: Department of Zoology, University of Melbourne, Parkville 3010, Australia

I-Min Tso: Department of Biology, Tunghai University, Taichung 407, Taiwan

ABSTRACT. We evaluated several formulae to estimate the capture area (the area of the web covered by capture spirals) and the mesh height (the distance between capture spirals) of orb webs constructed by *Argiope keyserlingi* Karsch. The accuracy of the various formulae was estimated through regression analyses. Accordingly, we propose two new formulae specifically suited for asymmetric orb webs, which provide accurate estimates of capture area and mesh height.

Keywords: Web architecture, web design, Araneidae, *Argiope keyserlingi*

The fundamental unit of behavior in orb-web spiders is the construction and design of the web. Web size and design can vary due to prey size (Sandoval 1994), food availability (Herberstein et al. 2000; Sherman 1994; Tso 1999), developmental stage (Higgins 1995; Heiling et al. 1998; Heiling & Herberstein 1998), physiological status (Eberhard 1988), web site (Eberhard 1989) and various abiotic factors (Vollrath et al. 1997). These web variations can directly influence the number and types of prey entangled. For example, a larger web will increase the rate of prey interception (Chacón & Eberhard 1980; Higgins & Buskirk 1992; Herberstein & Elgar 1994). Similarly, the distance between the capture spirals (mesh height) may affect the visibility of the web (Rypstra 1982; Craig 1986) and the size of prey entangled (Uetz et al. 1978; Murakami 1983; Miyashita & Shinkai 1995; Herberstein & Heiling 1998).

While the geometric nature of orb webs aids the measurement and consequent comparison of web elements such as web size and mesh height, these are sometimes difficult to obtain, particularly in the field. Therefore, some studies have used the length of the web radius (Higgins & Buskirk 1992) or web diameter (McReynolds & Polis 1987) as a very rough approximation of web size. Several recent studies have estimated web area with the help of formulae that require only a few measurements of the web (e.g., Nentwig 1985; Walker 1992; Sherman 1994). Regrettably, those studies do not provide a detailed description of the formulae used, nor do they estimate the accuracy of the generated values.

Recently Tso (1996) investigated the orb webs of *Argiope trifasciata* Forskål 1775 and estimated the capture area of the web (= the area covered by sticky spirals) and the mesh height using two formulae. Despite the detailed description of these formulae, Tso (1996) did not provide an account of how accurate the estimates were. Here we test the accuracy of several formulae to estimate capture area and mesh height by comparing the values derived from the formulae with exact values. Those tests will help validate surrogate variables and provide ecologists and ethologists with appropriate tools for estimating orb web parameters in the field.

METHODS

We used the webs of 11 adult female *Agriope keyserlingi* Karsch 1878 (built in 40 cm × 50 cm × 8.5 cm frames in the laboratory). The spiders were collected from suburban gardens in Brisbane, Australia and transferred to the laboratory in Melbourne, Australia. Each spider constructed one web, which was used for analysis (n = 11). Exact mesh height was obtained by measuring each distance between the spirals in the vertical upper and lower sector (Fig. 1). The values for both the upper and lower web halves were averaged for the mesh

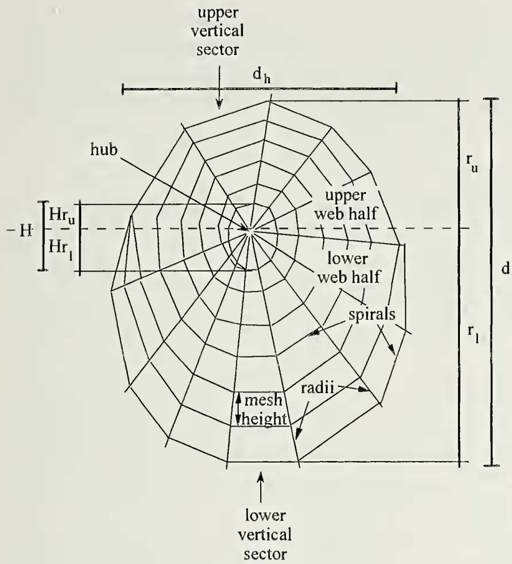

Figure 1.—A schematic representation (modified from Heiling & Herberstein 1998) of an asymmetric orb-web, defining the parameters used in the equations given by Tso (1996) and in this study. See text for symbols used.

height of the whole web. The exact capture area was obtained by summing the area covered by spirals in each web sector. The individual sector areas were calculated by treating each sector as a trapezoid, where the inner- and outermost spirals were assumed parallel. Although the inner and outer spirals may not always be perfectly parallel, we expect the consequent biases to be minimal. The exact capture area excluded the area of the hub, which is not covered by sticky spirals and therefore does not function in capturing prey.

To estimate the capture area of the webs, we considered several scenarios, which differed in the number of measurements taken from the webs. For example, a researcher may only know a single web diameter or may know all four web radii and the hub radii. We then developed formulae that are based on the available information and tested their predictive powers.

The 'Vertical Radii' formula (a) assumes a circular approximation of the web and estimates the radius from the vertical web diameter (d_v), which extends from the outermost spiral in the upper web half vertically through the hub to the outermost spiral in the lower web half (Fig. 1). The hub area is included in this formula.

(a) $(d_v/2)^2\pi$

The 'Vertical Radii − Hub' formula (b) estimates the 'true' capture area by subtracting the hub area, which is calculated using the vertical hub diameter (H). This diameter extends vertically from the innermost spiral in the upper web half to the innermost spiral in the lower web half (Fig. 1).

(b) $(d_v/2)^2\pi - (H/2)^2\pi$

The 'Ellipse' formula (c) assumes an elliptical approximation of the web and estimates both radii from the vertical and the horizontal diameter (d_h), respectively, but includes the hub area in its estimation. The 'Ellipse − Hub' formula (d) subtracts the hub area using the vertical hub diameter.

(c) $(d_v/2)(d_h/2)\pi$

(d) $(d_v/2)(d_h/2)\pi - (H/2)^2\pi$

The capture area formula (e; 'Tso − Hub') used by Tso (1996) calculates the web area of the upper and lower web halves separately using semi-circle approximations. It requires the upper (r_u) and lower (r_l) vertical radii, which extend from the hub to the outermost spiral in the upper and lower web half, respectively (Fig. 1). The area of the hub is calculated using the vertical hub diameter and subtracted to estimate the capture area.

(e) $$\left[\frac{1}{2}\pi r_u^2 - \frac{1}{2}\pi\left(\frac{H}{2}\right)^2\right] + \left[\frac{1}{2}\pi r_l^2 - \frac{1}{2}\pi\left(\frac{H}{2}\right)^2\right]$$

The 'Adjusted Radii − Hub' formula (f) is a modification of the 'Tso − Hub' formula. It also assumes a circular approximation treating each web half as semi-circles, but it adjusts the vertical radii by taking the horizontal diameter into consideration. Additionally, the hub area is calculated using the upper (Hr_u) and lower (Hr_l) hub radii separately. For this formula we required the upper and lower vertical radii, the horizontal diameter, the upper vertical hub radius and the lower vertical hub radius.

(f) $$\left[\frac{1}{2}\pi r_{au}^2 - \frac{1}{2}\pi(Hr_u)^2\right] + \left[\frac{1}{2}\pi r_{al}^2 - \frac{1}{2}\pi(Hr_l)^2\right]$$

Table 1.—The mean ± SE of the actual and the estimated capture area using various formulae which either include (+) or exclude (−) the area of the hub. The functional relationships between the actual and the estimated values are indicated using linear regression models with the SE of the regression slope given in parentheses. The F value indicates the significance of the regression model (Wilkinson 1992).

Estimate	Mean ± SE (cm^2) n = 11	Functional relationship	Significance
Actual capture area	555.8 ± 40.8		
Vertical Radii + Hub	628.2 ± 47.3	y = 207.9 + 0.6 (0.22) x; R^2 = 0.347	F = 6.3; P = 0.03
Ellipse + Hub	572.8 ± 33.6	y = −103.9 ± 1.2 (0.13) x; R^2 = 0.890	F = 82.2; P = 0.0001
Vertical Radii − Hub	547.2 ± 41.7	y = 206.2 + 0.6 (0.03) x; R^2 = 0.360	F = 6.6; P = 0.03
Tso − Hub	637.5 ± 48.5	y = 160.4 + 0.6 (0.19) x; R^2 = 0.493	F = 10.7; P = 0.01
Ellipse − Hub	491.9 ± 29.7	y = −96.8 + 1.3 (0.12) x; R^2 = 0.925	F = 124.5; P = 0.0001
Adjusted Radii − Hub	513.6 ± 30.7	y = −116.1 + 1.3 (0.08) x; R^2 = 0.965	F = 273.3; P = 0.0001

The adjusted upper (r_{au}) and lower (r_{al}) vertical web radii are:

$$r_{au} = \frac{r_u + \frac{d_h}{2}}{2} \qquad r_{al} = \frac{r_l + \frac{d_h}{2}}{2}$$

We tested two different formulae to estimate the average mesh height in orb-webs. The first (g) was previously published by Tso (1996) and it requires the upper and lower web radii, the hub diameter and the number of sticky spirals in the upper (S_u) and lower (S_l) web halves counted in the vertical sector directly above and below the hub (Fig. 1).

$$\text{(g)} \qquad \frac{1}{2}\left[\frac{\left(r_u - \frac{H}{2}\right)}{S_u} + \frac{\left(r_l - \frac{H}{2}\right)}{S_l}\right]$$

We modified this formula (h), using the upper and lower vertical hub radii rather than the hub diameter.

$$\text{(h)} \qquad \frac{1}{2}\left(\frac{r_u - Hr_u}{(S_u - 1)} + \frac{r_l - Hr_l}{(S_l - 1)}\right)$$

The formulae for capture area and mesh height were evaluated using regression analyses between exact values and their equivalent estimates generated by the formulae. Accordingly, an accurate estimate generates a high correlation coefficient (R^2). All analyses were performed using SYSTAT 5.2 for the Macintosh (Wilkinson 1992).

RESULTS AND DISCUSSION

Generating the capture area from the vertical diameter alone does not yield accurate estimates (Table 1). In contrast, estimates calculated by the 'Ellipse' formula are greatly improved. This is most likely to be due to the asymmetric nature of *A. keyserlingi* webs and indeed many other orb webs (Vollrath & Moren 1985; Vollrath 1987; Foelix 1992; Herberstein & Heiling 1999). Generally, orb webs are vertically elongated, particularly in the lower web half and the horizontal radii are shorter. Thus considering the horizontal diameters will improve estimates for asymmetric webs. Subtracting the hub area from the 'Vertical Radii' and 'Ellipse' formulae further improved these estimates (Table 1). Thus excluding the area of the hub from a capture area estimate is warranted for *A. keyserlingi* and species with similar webs. In those species, however, where the hub only takes up a smaller proportion of the web, it may be of minor importance.

Despite incorporating more web parameters than the 'Ellipse − Hub' formula, the 'Tso − Hub' formula did not yield as accurate estimates (Table 1). This is primarily due to web asymmetry, which also affects the hub region. Consequently, the capture area is generally

Table 2.—The mean ± SE of the actual and the estimated mesh height using formulae given in Tso (1996) and this study. The functional relationships between the actual and the estimated mesh height are indicated using linear regression models with the SE of the regression slope given in parentheses. The F value indicates the significance of the regression model (Wilkinson 1992).

	Mean ± SE (cm) $n = 11$	Functional relationship	Significance
Actual	0.45 ± 0.02		
Tso (1996)	0.39 ± 0.02	$y = 0.13 + 0.83\ (0.17)\ x$; $R^2 = 0.66$	$F = 19.96$; $P = 0.002$
This study	0.45 ± 0.02	$y = 0.02 + 0.95\ (0.07)\ x$; $R^2 = 0.95$	$F = 199.13$; $P = 0.0001$

overestimated, particularly in the lower web half. The most accurate estimates are generated by the 'Adjusted Radii − Hub' formula, because vertical asymmetry is being considered by incorporating the horizontal radii as well as calculating the upper and lower hub region separately (Table 1). Additionally, this formula generates separate values for the upper and lower web regions, which can be used for further analyses.

The mesh height formula used by Tso (1996) was not as accurate as our modified formula (Table 2) for two main reasons. First, Tso's (1996) formula uses the vertical hub diameter rather than the upper and the lower vertical hub radii separately, which introduces a bias in asymmetric webs. Second, the sector length covered by the sticky spirals is divided by the number of spirals, a common mistake (e.g., Sandoval 1994). Instead, this length should be divided by the number of spacings between the spirals, which equals the number of spirals minus one. This is particularly important for webs with few spiral spacings. Obviously, the accuracy of a mesh height formula could be further improved by sampling and incorporating additional web sectors.

The appropriateness of any web formula largely depends on the geometric nature of the web. Circular approximations such as the 'Vertical Radii − Hub' or the 'Tso − Hub' formulae, may accurately estimate capture area in symmetric and circular webs. Asymmetric webs with large hub areas however require more complex approximations, such as the proposed 'Adjusted Radii − Hub' formula.

ACKNOWLEDGMENTS

We are very grateful for the helpful comments provided by Norbert Milasowszky, Mark Elgar and the reviewers and editors of the Journal of Arachnology. Robert Raven provided helpful information about the location of the spiders. Doug and Sue Thiele gave permission to collect the spiders from their gardens. Diana Fisher and Simon Blomberg provided logistic support. Astrid Heiling and Volker Framenau helped with the formulae and the web graphic. John Mackenzie and Janet Yen provided flies for the spiders. MEH is supported by the Austrian Science Foundation through the postdoctoral grant J1318-BIO.

LITERATURE CITED

Chacón, P. & W.G. Eberhard. 1980. Factors affecting numbers and kinds of prey caught in artificial spider webs, with considerations of how orb webs trap prey. Bull. British Arachnol. Soc., 5:29–38.

Craig, C.L. 1986. Orb-web visibility: The influence of insect flight behaviour and visual physiology on the evolution of web design within the Araneoidea. Anim. Behav., 34:54–68.

Eberhard, W.G. 1988. Behavioral flexibility in orb web construction: Effects of supplies in different glands and spider size and weight. J. Arachnol., 16:295–302.

Eberhard, W.G. 1989. Effects of orb web orientation and spider size on prey retention. Bull. British Arachnol. Soc., 8:45–48.

Foelix, R.F. 1992. Biologie der Spinnen. Georg Thieme Verlag, Stuttgart.

Heiling, M.A. & M.E. Herberstein. 1998. The web of *Nuctenea sclopetaria* (Araneae, Araneidae): Relationship between body size and web design. J. Arachnol., 26(1):91–96.

Heiling, A.M., M.E. Herberstein & G. Spitzer. 1998. Calculation of the capture thread length in orb webs (Araneae: Araneidae): Evaluation of new formulae. Ann. Entomol. Soc. America, 91(1):135–138.

Herberstein, M.E., C.L. Craig & M.A. Elgar. 2000. Foraging strategies and feeding regimes: Web and decoration investment in *Argiope keyserlingi*

Karsch (Araneae: Araneidae). Evol. Ecol. Res., 2:69–80.

Herberstein, M.E. & M.A. Elgar. 1994. Foraging strategies of *Eriophora transmarina* and *Nephila plumipes* (Araneae: Araneoidea): Nocturnal and diurnal orb-weaving spiders. Australian J. Ecol., 19:451–457.

Herberstein, M.E. & A.M. Heiling. 1998. Does mesh height influence prey length in orb-web spiders? European J. Entomol., 95:367–371.

Herberstein, M.E. & A.M. Heiling. 1999. A symmetry in spider orb-webs: A result of physical constraint? Anim. Behav., 58:1241–1246.

Higgins, L.E. 1995. Direct evidence for trade-offs between foraging and growth in a juvenile spider. J. Arachnol., 23:37–43.

Higgins, L.E. & R.E. Buskirk. 1992. A trap-building predator exhibits different tactics for different aspects of foraging behaviour. Anim. Behav., 44:485–499.

McReynolds, C.N. & G.A. Polis. 1987. Ecomorphological factors influencing prey use by two sympatric species of orb-web spiders, *Argiope aurantia* and *Argiope trifasciata* (Araneidae). J. Arachnol., 15:371–383.

Miyashita, T. & A. Shinkai. 1995. Design and prey capture ability of webs of the spiders *Nephila clavata* and *Argiope bruennichii*. Acta Arachnol., 44:3–10.

Murakami, Y. 1983. Factors determining the prey size of the orb-web spider *Argiope aurantia* (Koch) (Argiopidae). Oecologia, 57:72–77.

Nentwig, W. 1985. Prey analysis of four species of tropical orb weaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone. Oecologia, 66:580–594.

Rypstra, A.L. 1982. Building a better trap; An experimental investigation of prey capture in a variety of spider webs. Oecologia, 52:31–36.

Sandoval, C.P. 1994. Plasticity in web design in the spider *Parawixia bistriata*: A response to variable prey type. Funct. Ecol., 8:701–707.

Sherman, P. 1994. The orb-web: An energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. Anim. Behav., 48:19–34.

Tso, I.M. 1996. Stabilimentum of the garden spider *Argiope trifasciata*: A possible prey attractant. Anim. Behav., 52:183–191.

Tso, I.M. 1999. Behavioral response of *Argiope trifasciata* to recent foraging gain: A manipulative study. American Midl. Nat., 141:238–246.

Uetz, G.W., A.D. Johnson & D.W. Schemske. 1978. Web placement, web structure, and prey capture in orb-weaving spiders. Bull. British Arachnol. Soc., 4:141–148.

Vollrath, F. 1987. Altered geometry of webs in spiders with regenerated legs. Nature, 328:247–248.

Vollrath, F. & W. Mohren. 1985. Spiral geometry in the garden spider's orb web. Naturwissenschaften, 72:666–667.

Vollrath, F., M. Downes & S. Krackow. 1997. Design variability in web geometry of an orb-weaving spider. Physiol. Behav., 62:735–743.

Walker, J.R. 1992. What do orb webs catch? Bull. British Arachnol. Soc., 9:95–98.

Wilkinson, L. 1992. SYSTAT: Statistics. Version 5.2. Evanston.

Manuscript received 10 May 1999, revised 20 September 1999.